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A KEY AND DESCRIPTION OF THE LIVING SPECIES
OF THE GENUS *PODOCNEMIS* (*SENSU* BOULENGER)
(TESTUDINES, PELOMEDUSIDAE)

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No. 8 — *A Key and Description of the Living Species of the Genus Podocnemis (sensu Boulenger) (Testudines, Pelomedusidae)*

By ERNEST WILLIAMS

Although *Podocnemis* (*sensu* Boulenger) is a genus of exceptional interest because of its distribution (South America and Madagascar), and because of the long fossil record ascribed to it (extending back to the Cretaceous), it has received little taxonomic attention since the review of the living species by Siebenrock in 1902. The need for such attention is well known. The keys provided by Boulenger (1889) and by Siebenrock (1902) are generally admitted to be unsatisfactory. Indeed in 1935 Lorenz Mueller, on the occasion of describing a new species *Podocnemis vogli* (thus raising the number of included species to eight), attempted a new key. This, however, has proved no more successful than the keys which preceded it.

At the urging of Mr. Llewellyn Price I have begun a study of the living species. I have thus far seen the material in the Museum of Comparative Zoology, the American Museum of Natural History, the United States National Museum, the Carnegie Museum, the Museum of Zoology of the University of Michigan, and the Chicago Natural History Museum, and I have also examined the material in the British Museum (Natural History), the Rijksmuseum, Leiden, the Senckenberg Museum, Frankfurt, the Museum für Naturkunde, Stuttgart, the Zoologische Staatssammlung, Munich and the Muséum d'Histoire Naturelle, Paris. I have seen also certain material from the Departamento de Zoologia, Sao Paulo, Brasil.

The revisionary task which I have set myself will be of interest to several sorts of individuals — to the naturalist in South America who desires to identify the forms he sees, to the museum worker in North America and in Europe concerned with labelling his specimens, to the student interested in the phylogeny, relationships and ancient migrations of these animals, and to the anatomist to whom some of the peculiarities (especially of the skull) in this and related genera will seem especially remarkable.

It will not be possible to satisfy these diverse interests in a single paper, and as a first step I am presenting here only a key

to the species. I am hopeful that the key will really permit ready recognition of all eight species, but I am hopeful also that a new and better key may stimulate interest in the genus and perhaps result in the acquisition of additional specimens of certain species (*cayennensis*, *vogli*, *lewyana*) which are all too rare in collections and which in consequence are incompletely known. Because of the inadequacy of our knowledge of these species the present is a preliminary and provisional effort.

The present key is unusually elaborate, and it is in effect a condensed description of the eight species presented in the form of a key. I have felt this to be desirable for several reasons.

First, the great individual variability of the members of this genus makes a simple key depending upon a few supposedly invariable characters nearly or quite impossible. The keys of Boulenger, of Siebenrock, and of Mueller have all failed because of the variability of supposedly diagnostic characters. I have indeed found some characters more constant than others, but I am unwilling to prophesy that *any* single character that I cite will not vary. The eight species of *Podocnemis* should be identified on the totality of the descriptions given.

Secondly, the fullness of the key should lessen errors due to any ambiguity of phrasing or to mere unfamiliarity with the characters in this genus. To still further decrease these opportunities for error I have included simple diagrams of certain key characters.

Finally the extreme fullness of the key is intended to permit recognition of juveniles as well as adults and of skeletons, or at least skulls, as well as alcoholies.

NOMENCLATORIAL REMARKS

The recent action of the Copenhagen Congress in adopting a 50-year rule in regard to preservation of commonly accepted specific names relieves this genus of its only nomenclatorial problem — the applicability of certain of the Schweigger names. In 1953 with the aid of M. Jean Guibé, I endeavored to discover the Schweigger types at the Paris Museum, but it quickly became evident that these types are now lost or mislabelled. Though Schweigger (1812) gives measurements for certain individuals of the species he names (and I would therefore regard these

measured individuals as the holotypes), in no case do the measurements check with any Paris specimen. The names therefore rest upon Schweigger's descriptions which, as is usual with descriptions of so early a period, are insufficient. It is fortunate to have available Siebenrock's 1902 paper as a fiat decision on the debatable Schweigger names.

Siebenrock's identification of *dumeriliana* Schweigger with *tracaxa* Spix is, in any case, quite certainly correct, and his adoption of the name *cayennensis* Schweigger for *erythrocephala* Spix is possible although not demonstrable. It is in some degree unfortunate that the Schweigger names now without types must be used in preference to those associated with the still extant and quite recognizable Spix types (seen at the Zoologische Staatssammlung, Munich), but if the Copenhagen rules are firmly adhered to, this situation will offer no real difficulty.

It must be stated that Siebenrock was in error in believing that *dumeriliana* of Boulenger was equivalent to his *cayennensis* = *erythrocephala* Spix. There is no *cayennensis* in the collections of the British Museum, and Boulenger recorded under this name some of the specimens of *unifilis* Troschel.

Bartlettia pitipiti Gray (type seen at the British Museum) is unquestionably a synonym of *P. sextuberculata* Cornalia.

Not having seen the type, I do not regard *P. continhii* Goeldi as assignable on the basis of the published description and figure (Goeldi 1886). Siebenrock's action in synonymizing this form with *P. lewyana* is unfortunate, since it extends the range of *P. lewyana* to the Amazon on grounds which seem quite inadequate.

I have examined the cotypes of *P. lewyana* A. Duméril in Paris. The two specimens belong to two species. The figured specimen (A. Duméril, 1852) from Bogotá, Colombia, presented by M. Lewy, is necessarily the holotype of *P. lewyana*, while the Venezuelan specimen belongs to *P. vogli* Mueller.

The species which I recognize are listed below with their most important synonyms:

1. *Podocnemis expansa* (Schweigger)

Synonyms: *Emys expansa* Schweigger 1812¹

¹ The Boulenger citation of the original publication of the Schweigger names is incorrect. See references cited below.

- Emys amazonica* Spix 1824
Podocnemis expansa Wagler 1830, Boulenger 1889, Siebenrock 1902
2. *P. cayennensis* (Schweigger)
Synonyms: *Emys cayennensis* Schweigger 1812
Emys erythrocephala Spix 1824
Podocnemis cayennensis Siebenrock 1902
3. *P. dumeriliana* (Schweigger)
Synonyms: *Emys dumeriliana* Schweigger 1812
Emys tracara Spix 1824
Emys macrocephala Spix 1824
Peltocephalus tracara Duméril et Bibron 1835
Podocnemis tracura Boulenger 1889
Podocnemis dumeriliana Siebenrock 1902
4. *P. unifilis* Troschel 1848
Synonyms: *Chelonemys dumeriliana* Gray 1870
Podocnemis dumeriliana Boulenger 1889
Podocnemis unifilis Boulenger 1889, Siebenrock 1902
5. *P. sextuberculata* Cornalia 1849
Synonyms: *Bartlettia pitipiti* Gray 1870
Podocnemis sextuberculata Boulenger 1889, Siebenrock 1902
6. *P. lewyana* A. Duméril 1852
Synonyms: *Podocnemis lewyana* Boulenger 1889, Siebenrock 1902
7. *P. madagascarensis* (Grandidier)
Synonyms: *Dumerilia madagascarensis* Grandidier 1852
Erymnochelys madagascarensis Baur 1888
Podocnemis madagascarensis Boulenger 1889, Siebenrock 1902
8. *P. vogli* L. Mueller 1935

I have seen very unequal numbers of these several species: over 300 *P. expansa*, over 100 *P. unifilis*, nearly 40 *P. sextuberculata*, about 20 *P. dumeriliana*, over 20 *P. madagascarensis*, 12 *P.*

lewyana, 15 *P. vogli*, and only 2 *P. cayennensis* — one of the latter the type of *Emys erythrocephala* Spix, the second a stuffed specimen in the Paris Museum. I have also notes on 5 additional specimens of *P. cayennensis* and 4 additional specimens of *P. dumeriliana* which have been examined for certain of their characters by Dr. J. Eiselt of the Naturhistorisches Museum, Vienna, for whose generous and courteous diligence I am deeply grateful.

It should readily be understood that our knowledge of certain of these forms still leaves much to be desired. I have not been able to see a skull of *P. cayennensis*, for example, and our information on the skull of this species is limited to a few remarks by Lorenz Mueller based on the skull of the type of *erythrocephala* Spix — a part of that type which was destroyed by fire during the Second World War. I have further not seen any of the forms in life, and my statements on color, taxonomically important at least in the young, are correspondingly limited. Information on species differences in habits and habitats is also much to be desired.

EXPLANATION OF TERMS USED

I have provided diagrams which should explain many of the terms used.

Thus certain of the most important types of head scalation are shown in Figure 1 A-II. I use the terminology of Siebenrock (1902).

For interpretation of the median notching of the upper jaw, see Figure 2 A-C.

The two principal conditions of the enlarged scales on the posterior borders of the hind feet are shown in Figure 3 A-B.

For the dorsal and ventral emargination of the temporal region of the skull see Figure 4 A-C. These figures show also the condition of the cavum tympani in three species — the size of the whole cavum tympani as compared with the orbit, the presence or absence of a precolumellar fossa, the relative size of the entrance to the post-otic antrum and the shape of the columellar foramen.

Figures 5-6 and 8-9 show palatal views of the seven species in which I have seen the skull. These views show the foramina incisiva, the maxillary ridges, the presence or absence of inter-

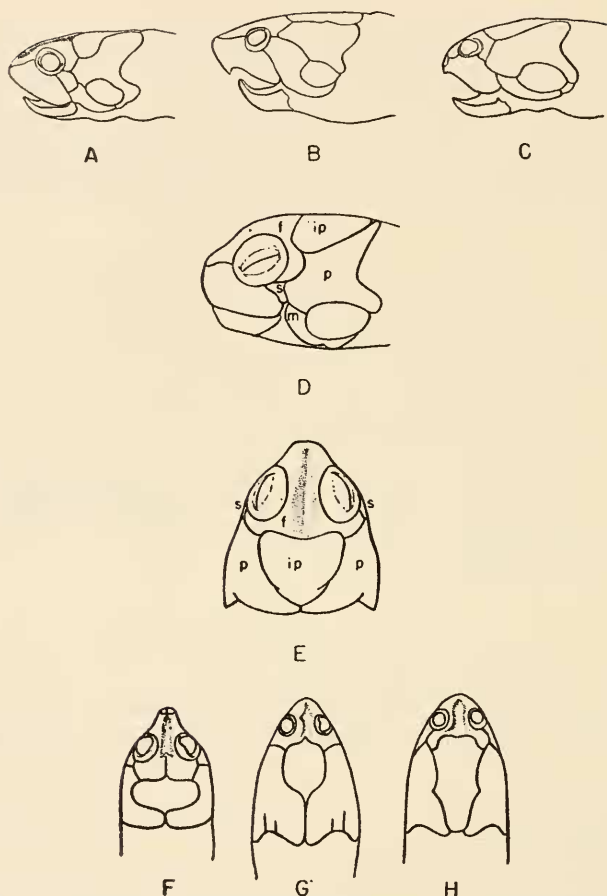


Fig. 1. Diagrams to show different conditions of the head scales. A, *P. unifilis* adult, lateral view — subocular present; B, *P. dumeriliana*, lateral view — masseteric reaching orbit; C, *P. expansa*, lateral view — frontal meeting maxillary; D, *P. unifilis* juv., lateral view. E, *P. unifilis* juv., dorsal view. F, *P. lewyana*, dorsal view — interparietal very broad, heart-shaped. G, *P. unifilis* adult, dorsal view — interparietal moderately elongate but parietals meeting behind it. H, *P. sextuberculata*, dorsal view — interparietal separating parietals. D and E original. A-C, F-H after Siebenrock (1902). Abbreviations: f, frontal scale; ip, interparietal; m, masseteric; p, parietal; s, subocular.

choanal bars, and the shape of the choanal opening.

Figure 7 shows the shape of the anterior lobe in four species and the length-width relations of the intergular scute in the same forms.

All figures are from specimens, except Figure 1, A-C and F-H which are after Siebenrock (1902).

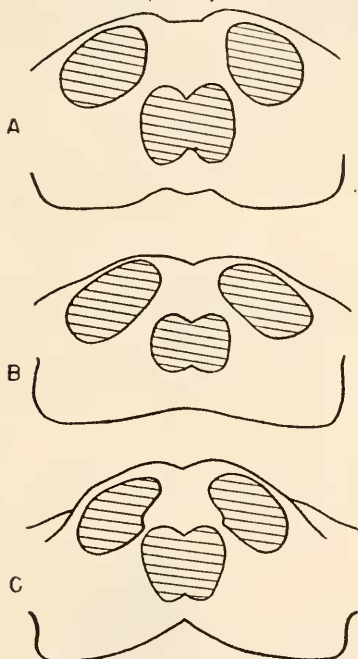


Fig. 2. Diagrams to show median notching of upper jaw. A, *P. expansa* — squared off, not rounded or notched. B, *P. lewyana* — rounded. C, *P. unifilis* — notched.

It is a pleasure to acknowledge the kindness of the authorities of the many museums listed above who have permitted me access to their collections or who have generously loaned specimens. I am indebted to Dr. Paulo Vanzolini and Mr. Benjamin Shreve who have tested my key and have pointed out some weaknesses in the original versions. Miss Patricia Washer is to be credited with the original sketches which illustrate this paper.

The opportunity to study the material in European collections was provided by a Guggenheim Fellowship 1952-1953.

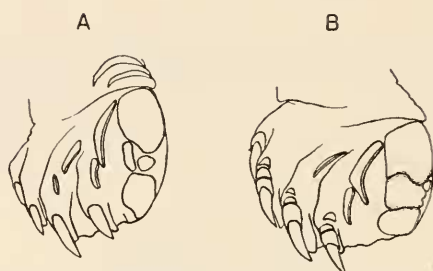


Fig. 3. Enlarged scales on posterior border of hind foot. *A*, *P. sextuberculata*—two scales. *B*, *P. unifilis*—three scales decreasing regularly in size.

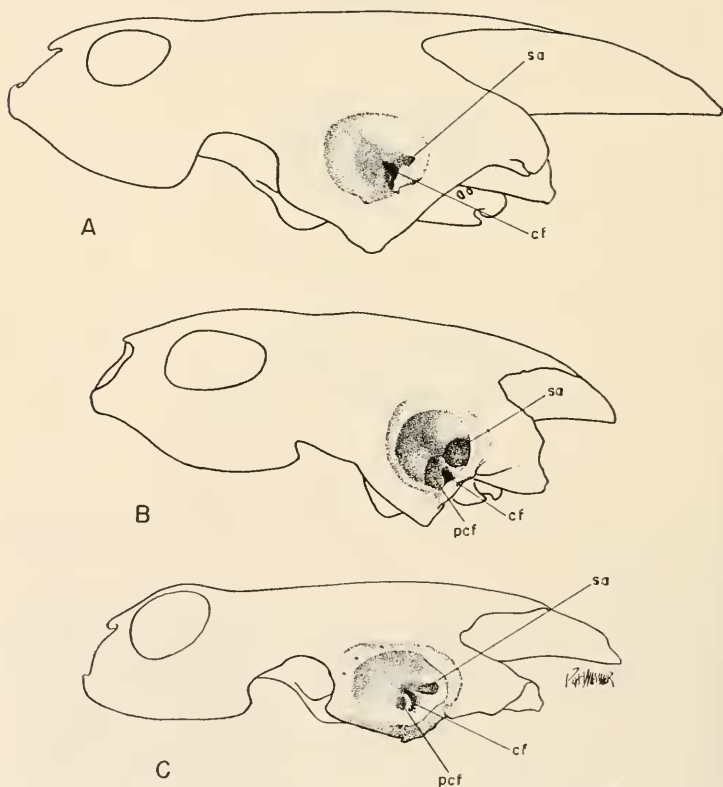


Fig. 4. Diagrams to show skull shape and ear region. *A*, *P. expansa* adult. *B*, *P. madagascarensis*. *C*, *P. unifilis*. Abbreviations: *cf*, columellar foramen; *pcf*, preeolumellar fossa; *sa*, post-otic antrum.

Key and description

1. Forehead grooved; masseteric scale not reaching orbit; dorsal surface of marginal six more than half as wide as long; jugal bone meeting parietal bone; quadrate bone not meeting jugal bone; temporal region of skull emarginate from below or not 2
Forehead convex; masseteric scale usually reaching orbit; dorsal surface of marginal six less than half as wide as long; jugal not meeting parietal; quadrate usually meeting jugal; temporal region of skull never emarginate from below 7
2. Upper jaw notched medially, if feebly notched the interparietal scale elongate; shell more or less convex 3
Upper jaw not notched medially, instead gently rounded or squared off; shell more or less flat 6
3. Notch of upper jaw continued to the nostril as a groove; interparietal scale very broad, heart-shaped even in adults; the first marginal scute long anteroposteriorly, as long or longer than wide. 5
Shell distinctly convex, much expanded posteriorly; vertebral keel distinct, most prominent on vertebral two or three. No nuchal indentation.
Skull elongate with two parallel longitudinal ridges on surfaces of the maxilla (*vide* L. Mueller, 1935).
Head scales: suboculars present.
Barbels: two.
Foot scales: two.
Color: Head reddish brown in individuals of *ca.* 250 mm. carapace length. Juvenile coloration unknown.
Size to 275 mm. (carapace length) *P. cayennensis* Schweigger
(Guianan and Amazonian regions and the Orinoco)
- Notch of upper jaw not continued to nostril as a groove; interparietal elongate, if at all heart-shaped only so in the very young; the first marginal scutes wider than long 4
4. Vertebral keel sharply raised into a swelling at the posterior margin of vertebral two; shell always smooth, concentric lines of growth if present few and usually lines of pigment only, not ridges on the horny shields. Hatchlings with three pairs of prominent swellings on the sides of the plastron, the axillary pair often still indicated in the adult.
Shell much expanded posteriorly. A nuchal indentation present, sometimes feeble.

Skull broad, a single feeble ridge on the triturating surface of the maxilla. Premaxillae separating maxillae and reaching the choanal margin. Vomer absent. No pre-columellar fossa in cavum tympani. Width of cavum tympani about equals width of orbit. Interorbital width less than height of orbit.

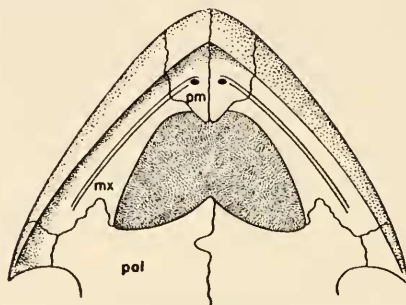


Fig. 5. Palate of skull in *P. sextuberculata*. Abbreviations: *mx*, maxilla; *pal*, palatine; *pm*, premaxilla.

Head scales: Interparietal scale usually widely separating parietal scales. Large suboculars present.

Barbels: two.

Foot scales: Three.

Size to 310 mm. *P. sextuberculata* Cornalia
(Amazonian region)

Vertebral keel never raised into a swelling at the posterior margin of vertebral two, shell often with concentric ridges. Hatchling never with three pairs of lateral swellings on the plastron 5

5. Vertebral keel usually distinct, typically most prominent on vertebral three; posterior shell margin somewhat expanded; shell commonly concentrically ridged. Size known to exceed 600 mm. Upper jaw distinctly notched. Skull elongate with two ridges on the triturating surface of the maxilla, the internal ridge not sharply dentate. Temporal region of skull strongly emarginate both dorsally and ventrally. Vomer usually absent.

Shell with a distinct nuchal indentation. Hatchlings with vertebral two usually only as long as vertebral three and with the plastron completely yellow or without a definite plastral pattern.

Skull more or less elongate. A deep preecolumellar fossa in the cavum tympani. Width of cavum tympani as great as or greater than the width of the orbit. Interorbital width less than height of orbit. Premaxillae not separating maxillae, not reaching choanal margin. Foramina incisiva well within the borders of the premaxillae. The interchoanal bar, if present, formed from the palatines.

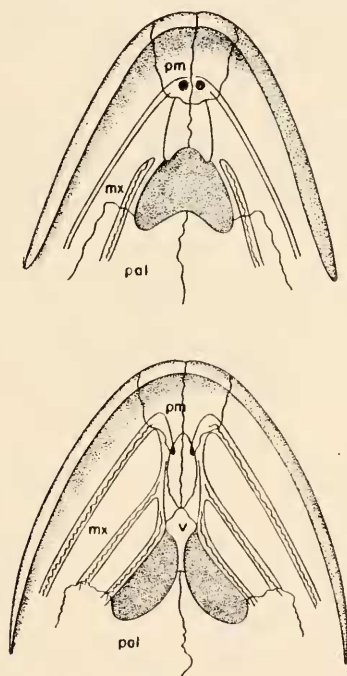


Fig. 6. Palates in *P. unifilis* (above) and *P. vogli* (below). Abbreviations as in Figure 5, with *v*, vomer.

Head scales: Interparietal scale very elongate but parietal scales usually meeting behind it. Suboculars usually present, usually not large. Maxillary scale light in color anteriorly and posteriorly, dark in the middle.

Barbels: Usually one.

Foot scales: Usually three.

Size to 680 mm. *P. unifilis* Troschel
(Guianan and Amazonian regions)

Vertebral keel feeble or absent; posterior margin of shell not expanded. Shields smooth or nearly so. Size not known to exceed 300 mm. Upper jaw feebly notched. Skull rather broad with three ridges on the triturating surface of the maxilla, all ridges roughened or dentate. Temporal region of skull well-covered, only slightly emarginate dorsally or ventrally. Vomer present, tending to form part of choanal septum.

Shell with only a feeble nuchal indentation. Hatchlings with vertebral two large, exceeding laterals three or four in length and with black quadrangular blotches on each plastral scute.

Skull rather broad. A precolumellar fossa present. Width of cavum tympani equals width of orbit. Interorbital width less than height of orbit. Premaxillae not reaching choanal margin but joining vomer to separate maxillae.

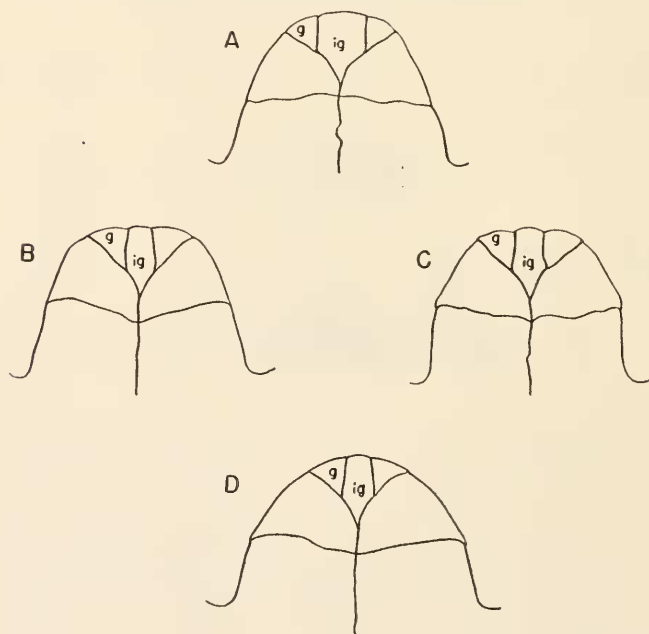


Fig. 7. Diagrams to show shapes of anterior lobes and of intergular scutes. A, *P. lewyana*. B, *P. vogli*. C, *P. unifilis*. D, *P. expansa*. Abbreviations: g, gular; ig, intergular.

Foramina incisiva well within margins of premaxillae but almost concealed from ventral view by extensions of the parachoanal triturating ridges.

Head scales: Interparietal scale elongate, but parietal scales meeting behind it. Suboculars large. Maxillary scale light only posteriorly, dark in middle and anteriorly.

Barbels: Two.

Foot scales: Three.

Size to 275 mm. *P. vogli* L. Mueller
(Venezuela, Orinoco drainage)

6. Intergular broad, gulars not longer than intergular is wide anteriorly. Head never with yellow spots on the interparietal scale, always with sides of head light in color.

Shell with vertebral keel barely or not at all visible. No nuchal indentation.

Skull moderately elongate, upper jaw rounded, not notched at middle. Two parallel ridges on the triturating surface of the maxilla. Width of cavum tympani equals width of orbit. Interorbital width less than height of orbit. Premaxillae not separating maxillae and not reaching choanal margin. Foramina incisiva well within the borders of the premaxillae. A vestigial vomer may be present.

Head scales: Interparietal scale heart-shaped. Suboculars present.

Barbels: Two.

Foot scales: Three.

Size to 411 mm. *P. lewyana* A. Duméril
(Colombia: Magdalena drainage)

Intergular narrow, gulars longer than intergular is wide anteriorly. Head at least in juveniles showing yellow spots on the interparietal scale.

Shell distinctly flattened, very large in adults. Vertebral keel usually not visible in adults, if visible most prominent on vertebral two very rarely most prominent on vertebral three. Horny shields weakly or not concentrically ridged. No nuchal indentation. Hatchling with vertebral three extremely broad and short, up to three times as broad as long, always shorter than vertebrals two or four. Vertebral two as long as or longer than vertebral four. Sometimes first marginals as long as wide, usually wider than long.

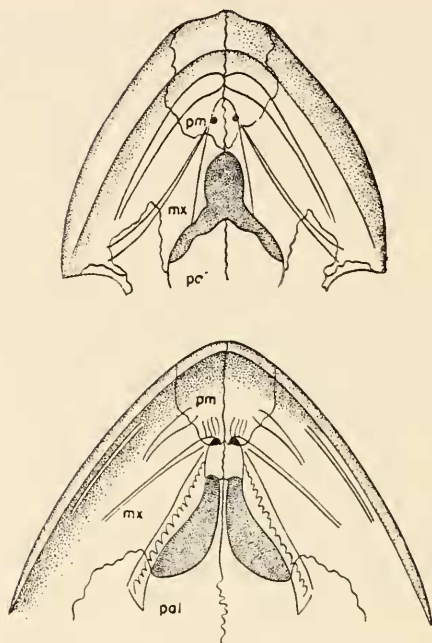


Fig. 8. Palates in *P. lewyana* (above), and *P. expansa* (below). Abbreviations as in Figure 5.

Skull broad in adults, less so in young, upper jaw squared off at tip rather than rounded or notched. Two or three ridges on the triturating surface of the maxilla, the first very short, originating from the premaxilla, the second much longer but parallel to the first, the third, if present, parachoanal, diverging strongly from the other two. Another very feeble ridge placed on the inner side of the outer vertical cutting surface of the maxilla. Width of cavum tympani greater than width of orbit. Interorbital width less than height of orbit. Premaxillae not separating maxillae, not reaching choanal margin. Foramina incisiva at caudal margin of premaxillae, a small area of bone anterior to the foramina wrinkled. Vomer absent. Palatines usually forming choanal septum and reaching maxillae anteromedially. Precolumellar fossa in cavum tympani absent or feebly indicated, except in

young in which it may be well developed. Entrance to post-otic antrum narrowed in adults.

Head scales: Interparietal scale tapering posteriorly, separating the parietal scales or not. Usually frontal scale in contact with maxillary scale and suboculars absent.

Barbels: Usually two.

Foot scales: Usually two, if three, middle scale smallest.

Size to 820 mm. *P. expansa* Schweigger
(all northern South America east of the Andes, and the Magdalena drainage)

7. Interparietal scale expanding posteriorly. Upper jaw strongly hooked. Femoral median sulcus longest. Humeral usually about as long as pectoral. Intergular usually larger than gulars.

Shell convex, vertebral keel strong on last two vertebrae.

First marginal not wider than long. Shields with numerous concentric growth rings, sometimes also with radiating striae. Supracaudals sometimes united.

Skull triangular. A single feeble ridge on the triturating surface of the maxilla. A deep anterior premaxillary fossa. Premaxillae usually separating maxillae and reaching choanal margin. Foramina incisiva well within the borders of the premaxillae. Vomer absent. A vertical poorly defined precolumellar fossa. Width of cavum tympani equal to or greater than width of orbit. Interorbital width greater than height of orbit.

Head scales: Interparietal scale widely separating parietal scales. Masseteric scale so far as known always reaching maxillary.

Barbels: One.

Foot scales: Three.

Size to 480 mm. *P. dumeriliana* Schweigger
(Guianan and Amazonian regions)

Interparietal scale tapering posteriorly. Upper jaw feebly hooked. Abdominal median sulcus longest. Humeral much shorter than pectoral. Intergular very small, gulars uniting behind it.

Shell convex, a vertebral keel not discernible in adults.

First marginal broader than long. Shields with numerous concentric growth rings and radiating striae.

Skull broad. A single feeble ridge on the triturating surface of the maxilla. Premaxillae separating maxillae

and reaching choanal margin narrowly or maxillae barely meeting and separating premaxillae from choanal margin. Foramina incisiva well within the borders of the premaxillae. A vertical precolumellar fossa present in cavum tympani. Width of cavum tympani less than width of orbit. Interorbital width about equal to height of orbit.

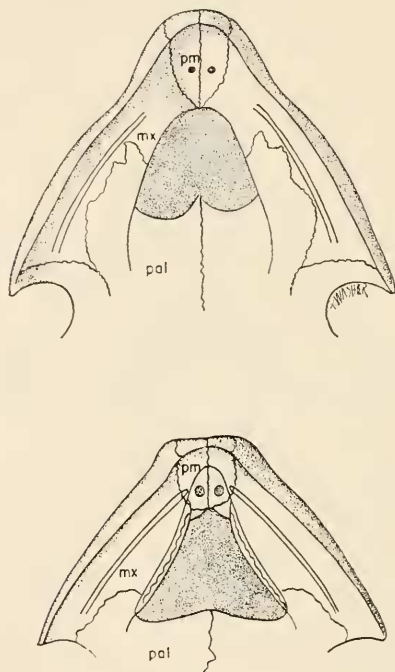


Fig. 9. Palates in *P. dumeriliana* (above), and *P. madagascarensis* (below). Abbreviations as in Figure 5.

Head scales: Interparietal scale tapering posteriorly, parietal scales meeting behind it. Usually masseteric scale reaching maxillary scale, but sometimes suboculars present.

Barbels: One, rarely two.

Foot scales: Three.

Size to 435 mm. *P. madagascarensis* Grandidier
(Madagascar)

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